UNDERSTANDING SIZE AND PATTERN VARIATION IN
MAINLAND BRITAIN *PARARGE AEGERIA* L.
(LEPIDOPTERA: SATYRIDAE)

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The Speckled Wood butterfly, *Pararge aegeria* L., is represented in England, Wales and N.E. Scotland by subspecies *tircis* Butler, and in N.W. Scotland by subspecies *oblita* Harrison (Thomson, 1980). Adult *P. a. oblita* are larger than *P. a. tircis* (Thomson, 1980; Brakefield & Shreeve, 1992), but latitudinal size variation within mainland Britain has not been extensively examined. Thompson (1952) reported an altitudinal cline in Snowdonia, culminating at high altitude in large, prominently marked specimens and designated form *drumensis*, but no further investigation into the form has been conducted.

The present paper examines latitudinal and altitudinal size variation in the species within mainland Britain, comparing cohorts from S. England, low and high altitude in N. Wales, and N.W. Scotland, at 14°, 17° and 20°C under 16 hours (16 h) daylength. The environmental and hereditary factors underlying the clines, and the adaptive significance of the size variation, are considered. A new eyespot aberrant from N. Wales is characterized and the gene frequency at each altitude is estimated. The occurrence of ab. *cockaynei* Goodson (Russwurm, 1978) and 'spring brood' forms (Robertson, 1980a) among N. Wales *P. a. tircis* and *P. a. oblita* undergoing pupal diapause at 14°C is discussed, and an explanation of form *drumensis* is proposed. The present findings represent a more extensive account of *P. aegeria* specimens presented at the 1993 BENHS Annual Exhibition, and complement a study into clinal variation in life history traits (Sibly *et al*, in prep.).

MATERIALS AND METHODS

Adult *P. aegeria* were collected from the Isle of Appin, Scotland (56° 32′ N, 5° 24′ W) on 14.viii.1992, at 50–60 m above mean sea level (amsl) (Gorswen, 53° 13′ N, 3° 51′ W) and 200–220 m amsl (Hafod-y-cae, 53° 13′ N, 3° 54′ W), from the S.E. face of Tal-y-fan mountain, N. Wales, between 17–21.viii.1992, and from the west of Salisbury Plain, S. England (51° 13′ N, 1° 39′ W) on 4.ix.1992. They were transferred to the laboratory 9 days after capture (Scotland), 2–6 days (Wales) or 1 day after capture (England).

Pairs were maintained in 2½" diameter card tubs lined with untreated tissue and covered with fine-mesh netting secured with elastic. Adults were fed 5% vol/vol unmodified honey solution from cotton pads placed on the netting. Pads were replaced daily. When females started ovipositing on the netting and tissue, the males were killed. Oviposition was continued in the laboratory at 20°C.

Ova from each female were collected daily and divided between 14°, 17° and 20°C constant temperature regimes under 16 hours light : 8 hours dark photoperiod provided by fluorescent lighting of spectral composition approximating daylight. Egg samples from a given female were held in 3" × 2" × 1" transparent perspex boxes until hatched. Ten larvae per female per temperature (30 per female) were segregated (i.e. one larva per box) to similar boxes containing excess cultivated cock's-foot grass, *Dactylis glomerata* L. The 30 larvae per female were randomly collected to ensure that they reflected the genetic make-up of the total egg batch; the excess larvae were

dispersed elsewhere. Boxes containing pupating larvae were cleared of food and oriented so that the prepupae hung vertically. Representative adults were killed and preserved.

LATITUDINAL VARIATION

At all three temperatures, adults of *P. a. oblita* were the largest and S. England *P. a. tircis* the smallest, indicating a progressive increase in size with distance north. Within each stock, adults were noticeably larger at 17° than 20°C, following the general tendency of ectotherms to attain greater mature weights at lower temperatures, and probably related to slower growth under cold (Atkinson, 1994). However, adults were slightly smaller at 14° than 17°C, especially in S. England *tircis* but this difference became less marked with latitude.

In *P. aegeria*, the photoperiodic cue governing developmental strategy comprises the interval sunrise to sunset, and possibly also morning and evening twilights, during the first and final larval instars (Nylin *et al*, in press). At the latitudes compared here, daylengths of 16 h or more prevail through May to July, when the collected animals would have been larvae (Goddard, 1962). Mean daily temperature in 1992 declined by ~1°C per degree increment in latitude (Table 1). Given the temperature gradient alone, field-collected adults would be expected to be larger at the more northerly sampling sites, as found by Brakefield & Shreeve (1992). However, the persistence at each culture temperature of a latitudinal size cline in the adult form predicted on the basis of a latitudinal gradient in field temperature, suggests that developmental strategies originally governed by temperature alone have become genetically determined. This suggests that selection could act on individuals whose size is 'adaptive' in the respective environment, to build up a genetic pattern in which individuals attain similar sizes even when 'transplanted' to alternative environments, a process Waddington (1961) termed 'genetic assimilation' and defined as 'an increase in the importance of heredity in the extent to which a character is determined by heredity and by the environment'.

The speckled wood basks in sunshine to raise body temperature to levels enabling flight (Shreeve, 1986). In N.W. Scotland where air temperatures are cooler (Table 1) and cloud cover is more prevalent (Thomson, 1980), large specimens would retain

Table 1. Periods in 1992 comprising daylengths (sunrise to sunset, and including morning and evening civil twilights) or 16 h or more at the three sampling sites, and mean (±SD) daily temperatures (°C) at proximal weather stations over the corresponding periods.

	S. England Salisbury Plain	N. Wales Tal-y-fan Mountain	N.W. Scotland Isle of Appin
≥16 h day:	24.v–18.vii	18.v–25.vii	9.v–3.viii
≥16 h day + twilights:	30.iv–12.viii	26.iv–16.viii	20.iv–22.viii
	Middle Wallop 51° 9′ N, 1° 34′ W 90 m amsl	Colwyn Bay 53° 17′ N, 3° 43′ W 36 m amsl	Greenock MRCC 55° 58′ N, 4° 48′ 5 m amsl
Temperature (°C) April:	—	10.0 ± 3.4	9.1 ± 2.9
May:	14.0 ± 6.8[1]	13.5 ± 5.9	12.6 ± 5.3
June:	15.9 ± 6.5	14.6 ± 4.2	15.2 ± 4.1
July:	17.0 ± 4.6	15.7 ± 3.7	14.9 ± 3.9
August:	18.1 ± 5.1	15.6 ± 3.2	14.3 ± 3.1

[1]Includes data for 30.iv.1992.

body heat for longer thereby maximizing oviposition and mate locating activity; larger males may also be better at defending territories (Davies, 1978). The smaller size of Hampshire specimens may result from their faster larval growth (Sibly *et al*, in prep.), not only facilitated by warmer summer temperatures, but possibly adaptive in minimizing their period of exposure to predation, parasitism and disease (Smith *et al*, 1987), and in enabling rapid population recovery following losses through drought (Thomas & Webb, 1984); *P. aegeria* is at least bivoltine throughout its British range (Goddard, 1962; Thomson, 1980).

The smaller sizes of adult *P. aegeria* attained at 14° than 17°C, especially in the case of S. England *P. a. tircis*, would appear to violate the expected increase in size with cooling temperature (Atkinson, 1994). A tentative explanation is that larvae are less efficient at utilizing food at 14°C than 17°C. In S. England, as the season progresses, daylengths of 16 h or more prevail and air temperatures rise (Table 1), and incident sunlight enables the larvae to utilize metabolic resources efficiently. In N.W. Scotland, where temperatures are cooler and cloud cover is more prevalent, larval physiology in *P. a. oblita* may be adjusted to utilize metabolic resources more efficiently at cooler temperatures. In the present study where daylight was simulated by a cold light source, the metabolic efficiency of *P. a. tircis* at 14°C (compared to that at 17°C) may have been considerably more compromised in the absence of supplementary radiant heat. Indeed the smaller size attained by *P. a. tircis* at 14° than at 17°C despite larval growth being the more protracted at 14°C (Sibly *et al*, in prep.), would concur with this hypothesis.

Nylin & Svärd (1991), in a study of museum specimens, found that *P. a. tircis* in Sweden, showed a decrease in size with distance north; they also found a decrease in size northwards from central Europe. Although contradicting the findings of Brakefield & Shreeve (1992), Nylin & Svärd (1991) argue that at more southerly latitudes, specimens should be larger because of the greater prevalence over the year of air temperatures above a critical temperature for larval growth, and hence a longer growing season.

However, one might expect growth to be faster under the higher temperatures, resulting in smaller adults but more annual generations. Moreover, under hot regimes (and especially in central Europe where a more 'continental' climate prevails than further west), larvae may aestivate to survive food stress during drought, with protracted larval durations but less time spent growing. Since a number of low altitude N. Wales male *P. a. tircis* at 20°C showed larval periods of 9–10 weeks (compared to the norm of 4–5 weeks) yet if anything emerged lighter in weight (Sibly *et al*, in prep.), their protracted development may represent such a strategy. Although corresponding larval durations were undergone at 20°C by a number of female *P. a. oblita*, such 'slow' individuals emerged heavier than the faster growing ones (Sibly *et al*, in prep.) indicating a different strategy and suggesting that even under hot summers *P. a. oblita* would continue to emerge larger than English *P. a. tircis*.

Latitudinal size trends in *P. aegeria* are further complicated by shifts in voltinism (Nylin & Svärd, 1991), and where the species is multivoltine, by seasonal differences in climate (Robertson, 1980a). The author proposes that rather than the butterfly showing a simple latitudinal cline, the smallest adults result where conditions are most *extreme*. Accordingly one would expect smaller adults under Continental and 'Arctic' than oceanic conditions. By way of example N.W. Scotland *P. a. oblita* enjoy an 'oceanic' climate with cool summers and largely frost-free winters (Thomson, 1980). In N. Sweden *P. a. tircis* suffers more extreme conditions. It experiences cooler summers and winter temperatures that rarely rise to levels allowing larval growth

(Nylin & Svärd, 1991). Here, the species is univoltine, the larvae aestivating when summer temperatures are cool (rather than the adult emerging the same season) and pupating in the autumn (Wiklund *et al*, 1983). Swedish univoltine populations lie at the northern limit of the species range (Brakefield & Shreeve, 1992), where aestivation may help the larva cope with less efficient nutrient utilization, and the early autumn pupation may enable the animal to withstand winter frosts. Under the Continental conditions of central Europe where there are extremes of heat, and especially where associated with drought, aestivation may enable larvae to survive food shortages. With more oceanic regimes such as in N.W. Scotland, hot summers may be less prone to drought, and hence larval diapause less critical to survival. Indeed, the protracted development and heavier weight of 'slow' *P. a. oblita* at 20°C (compared to 'fast' *P. a. tircis*) (Sibly *et al*, in prep.), accords with this hypothesis. Detailed examination of the temperature ranges over which temperature, larval period and adult size show direct correlation (in the present study between 17° and 20°C), of individual instar durations and dimensions, and of larval growth curves, would further clarify the factors determining latitudinal size trends in non-migratory species such as *P. aegeria*.

ALTITUDINAL COMPARISONS

There was no obvious difference in adult size between low and high altitude N. Wales *P. a. tircis* at any of the study temperatures. Sibly *et al* (in prep.) similarly found no significant differences in body weight (nor in other components of life history), suggesting that the larger size (and more extensive pale markings) of the high altitude '*drumensis*' forms described by Thompson (1952), may have been simply a consequence of their having developed under cooler temperatures than their low altitude counterparts (Geiger, 1965; Table 1). Some features of the present N. Wales samples are now considered to determine further the nature of any altitudinal effects.

Spot-pattern aberration

Two of the 21 wild high-altitude females and one of the 21 wild low-altitude females originally taken between 17 and 21.viii.1992 displayed an eyespot or *ocellus* element (Schwanwitsch, 1935) in ventral forewing space 2 additional to that in space 5. The phenotype does not appear to have been previously documented. Since the forewings correspond to the mesothoracic segment (Sibatani, 1980), it is suggested that the phenotype be designated *mesoventro-s2/s5 biocellata* ab. nov. (Plate I, Figs. 13–15). The phenotype appeared at all three temperatures among the F_1 of both stocks and in both sexes, indicating that the allele is autosomal (i.e. not carried on the sex chromosomes), and since the low-altitude ab. *mesoventro-s2/s5 biocellata* female #9 yielded all wild-type F_1 (12 in all), also recessive; a dominant allele would predict at least 50% *biocellata* phenotypes among the F_1 (Falconer, 1981).

GENOTYPE FREQUENCIES, LOW ALTITUDE. Calling the wild-type allele '*W*' and the recessive *biocellata* allele '*b*', low-altitude female #9 was probably *bb* and the male most likely *WW*. Low-altitude wild-type female #5, however, yielded 9 out of the 30 F_1 of which 3 (33%) were aberrant; low altitude female #5 was probably *Wb*, and the male most likely *Wb* (a *bb* male would predict a 1 : 1 ratio of aberrant to wild-type). Of the 19 remaining low-altitude females, only 9 yielded an F_1 generation. These were wild-type and yielded all wild-type offspring. If these females were *Wb* they would necessarily have paired with *WW* males, while if *WW* they could have

paired with *WW*, *Wb* or *bb* males. Minimum and maximum estimates of *biocellata* allele frequency within the low-altitude parent sample can be estimated using the F_1 results of these 11 females. Based on the assumption of 9 *WW* × *WW* pairings (lower estimate) and 9 *WW* × *bb* (upper estimate) and taking into account females #5 (*Wb* × *Wb*) and #9 (*bb* × *WW*), the following can be expected.

Lower estimate. The lower estimate assumes 9 *WW* × *WW*, 1 *Wb* × *Wb* and 1 *bb* × *WW* pairings, involving $(1 × bb) + (2 × Wb) + (19 × WW)$ genotypes comprising 4 '*b*' and 40 '*W*' alleles, and hence a *biocellata* gene frequency of 4/44 (9.1%) with 3/22 (13.6%) of individuals carrying the gene.

Upper estimate. The upper estimate assumes 9 *WW* × *bb*, 1 *Wb* × *Wb* and 1 *bb* × *Wb* pairings, involving $(10 × bb) + (2 × Wb) + (10 × WW)$ genotypes comprising 22 '*b*' and 22 '*W*' alleles, and hence a *biocellata* gene frequency of 22/44 (50%) with 12/22 (54.5%) of individuals carrying the gene.

GENOTYPE FREQUENCIES, HIGH ALTITUDE. High altitude *mesoventro-s2/ s5 biocellata* females #1 and #5 were most likely *bb*. Both yielded aberrant F_1 (3 out of 15 individuals (20%) and 11 out of 26 (42%) respectively), the male parents therefore having been most likely *Wb* (*bb* would predict an all aberrant F_1 and *WW* an all wild-type F_1). The lower than expected frequency of *biocellata* phenotypes predicted from a *bb* × *Wb* cross may indicate a greater mortality among *bb* genotypes. The 13 remaining females to yield F_1 were wild-type and yielded all wild-type offspring.

Lower estimate. The lower estimate of *biocellata* gene frequency in the high-altitude population assumes 13 *WW* × *WW* and 2 *bb* × *Wb* pairings, involving $(2 × bb) + (2 × Wb) + (26 × WW)$ genotypes comprising 6 '*b*' and 54 '*W*' alleles, and hence a *biocellata* gene frequency of 6/60 (10%) with 4/30 (13.3%) of individuals carrying the gene.

Upper estimate. The upper estimate of *biocellata* gene frequency in the high altitude population assumes 13 *WW* × *bb* and 2 *bb* × *Wb* pairings, involving $(15 × bb) + (2 × Wb) + (13 × WW)$ genotypes comprising 32 '*b*' and 28 '*W*' alleles, i.e. a *biocellata* gene frequency of 32/60 (53.3%) with 17/30 (56.7%) of individuals carrying the gene.

Population structure and gene flow

Since the field collected males from both altitudes displayed wild-type pattern when the *biocellata* gene is autosomal (i.e. not sex-linked), the actual gene and genotype frequencies in the wild populations probably lie nearer the lower estimates. However, the occurrence in samples from both altitudes of similar lower and upper estimates, suggests that individuals along the altitudinal gradient function as a single population. Although the sampling sites represented separate woodlands, each woodland was contiguous between 30 and 200 m amsl. Furthermore, maximum separation between these woodlands was ~400 m, yet female *P. aegeria* can disperse up to 600 m and traverse open terrain (Davies, 1978). Thus, while genetic assimilation has been implicated in the evolution of high-altitude forms elsewhere (Shapiro, 1976), gene flow between low- and high-altitude *P. a. tircis* in N. Wales may limit such altitudinal differentiation here.

Pupal diapause

Among the high altitude stock at 14°C, 6 of 87 F_1 individuals (7%) underwent pupal durations greater than 28 days indicative of diapause (Lees & Tilley, 1980). Of these 6 high-altitude diapause pupae, 3 males and 1 female (67%) emerged as ab.

cockaynei Goodson, in which the dark underside wing areas tend to merge and appear more uniform, contrasting vividly with the remaining pale markings and eyespot pupils (Russwurm, 1978: Plate 32) (Plate I, Figs 16–17). Diapause pupae appeared in the low altitude stock however, only after *two* generations at 14°C (2 diapause pupae, total of direct developing pupae not ascertained).

An earlier study using S. England *P. a. tircis* under 16 h daylength (Winokur, 1992), had found that the offspring of individuals reared at 18°C yielded only direct developing pupae at both 14° and 18°C, but that if the parents were briefly chilled as pupae to $-2°C$, then some of the offspring reared at 14° (but not 18°C) underwent diapause to emerge as ab. *cockaynei*. Since British *P. a. tircis* typically form diapause pupae only under daylengths of 11 h or less irrespective of temperature (Lees & Tilley, 1980), it was concluded that pupal diapause and pattern modification at 14°C with 16 h daylength depended on the parents having experienced pupal frost, thereby implicating some parental effect. Considering again the N. Wales low altitude *P. a. tircis*, it is proposed that diapause in the F_2 at 14°C with 16 h could similarly have been conditioned by the parents too having developed at 14°C. While Colwyn Bay meteorological station (36 m amsl) recorded a July mean of 15.7°C (Table 1), higher altitudes would be expected to be cooler (Geiger, 1965), hence a number of the high-altitude parental sample (collected at 200–220 m amsl) might have developed at 14°C (or cooler). Higher altitudes would also be expected to suffer more prevalent winter frosts (Geiger, 1965), and while this would be of more direct consequence to individuals of generation 1, sporadic summer frosts at high altitude cannot be ruled out.

P. a. tircis mesoventro-s2/s5 biocellata. F_2 from a high altitude F_1 *mesoventro-s2/s5 biocellata* female reared at 20°C (female #1.4), were cultured indoors from 11.x.1992 in 5" diameter translucent perspex tubs, under natural daylength but away from direct sunlight, and replenished with cut foodplant at two-day intervals. Room temperature was not recorded but might be expected to be warmer than in the field. Only three pupae diapaused, yielding two 'early spring' form males (Plate I, Fig. 14); and a *cockaynei* female (Plate I, Fig. 15) which may have been 'forced' by indoor temperature.

Diapause comparisons with subspecies oblita

Of the *P. a. oblita* F_1 at 14°C, 36 of 52 pupae (70%) diapaused, but of 24 diapause adults preserved only 3 males and 1 female (17%) were ab. *cockaynei* (Plate I, Fig. 18); the remainder were typical 'early spring' forms (Plate I, Fig. 19). Direct developing *P. a. oblita* were of the late spring/summer form that typify the 2nd brood (Plate I, Fig. 20; Robertson, 1980a), suggesting that 'early spring' phenotype in *P. aegeria* is linked to pupal diapause; linking of vernal phenotype to diapause is known in other species (Shapiro, 1976).

Aberrant pattern in North Wales (and S. England) *P. a. tircis*, may have resulted from the 16 h daylength being atypical of times in their season when prevailing temperature is 14°C or less (Table 1). Hence the atypically long photoperiod may have 'forced' pupae that at 14°C or less would normally have been diapausing under shorter associated daylengths.

At the latitude occupied by *P. a. oblita* on the other hand, daylengths of 16 h or more persist later into the season, when concomitant temperatures would be cooler than further south (Table 1) thereby leaving less time for the animals to complete the life cycle before winter. Hence in *P. a. oblita*, one might expect the critical photoperiod for pupal diapause to be shifted to longer daylengths than for more southern *P. a. tircis* (cf. Nylin *et al*, in press); with 16 h daylength therefore being

closer to the normal photoperiodic cue for diapause in *P. a. oblita* and so less likely to result in aberrant wing pattern.

UNDERSTANDING AB. *COCKAYNEI* AND '*DRUMENSIS*' FORMS

The incidence of ab. *cockaynei* among the respective cohorts points against chance genetic mutation, and suggests that development of the phenotype does not depend on a particular genotype *per se*, but rather is a structured response of the wing developmental physiology to a variety of atypical cytogenetic–environmental interactions. Several examples of *cockaynei* are known e.g. Rothschild-Cockayne-Kettlewell collection, British Museum (Natural History), and it may represent a 'recurrent' aberration (cf. Shapiro, 1975). *P. aegeria* larvae often pupate in exposed locations and show little inclination to seek shelter (Cole, 1962), and *cockaynei* individuals may represent the progeny of animals subjected to frost as young pupae. The parental frost exposure might result in the progeny larva undergoing protracted growth, but nevertheless reaching the final instar under daylengths of 16 h or more. While 16 h daylength would normally cue direct pupal development, the parental history could result in the individual undergoing atypical diapause, the adult possibly emerging in late autumn if temperatures permit but otherwise perishing as a pupa; the specimen figured by Russwurm (1978) was taken in November.

Should the progeny larva not reach the final instar until later in the autumn, the shorter daylength itself would cue pupal diapause and associated 'early spring' phenotype. The parental history may further protract the diapause, so that the 'early spring' form thus emerges later than the usual April–May of generation 1 part *i* (Goddard, 1962) as with '*drumensis*' which Thompson (1952) reported as flying above the tree line in June.

In the present study, diapause individuals from high altitude *P. a. tircis* and Scottish *P. a. oblita*, also grew more slowly as larvae and produced heavier adults (Sibly *et al*, in prep.). Thus protracted larval development in putative '*drumensis*' (*P. a. tircis*) individuals could account for their larger size. Indeed, Thompson's specimens may have resembled vernal *P. a. oblita* (Plate I, Fig. 19), for N. Wales *P. a. tircis* and *P. a. oblita* diapause animals showed similar pupal durations and male weights (Sibly *et al*, in prep.).

Alternatively, *drumensis* may simply have constituted an unusually late generation 1 part *ii*, which flies in late May/June (Goddard, 1962) and typically comprises the largest adults of all the broods (Robertson, 1980a). Such *drumensis* may have resembled somewhat 'late spring' *P. a. oblita* specimens (Plate I, Fig. 20), though without Thompson's specimens for comparison further field work is required to reliably characterize the form. Reasons for the absence of subsequent reports include the failure to conduct any further planned studies, and it is therefore important not to discount *a priori* the natural occurrence of '*drumensis*'. Second, since its occurrence would appear to depend on prevailing climate, fluctuations in the prevailing weather between years (Shreeve, 1986) may result some years in the form being absent. Third, being described from atypical habitat (open grassland/moor, pers. obs.) where recorders are unlikely to be monitoring the species, it is liable to be overlooked. Finally, its June flight period means that collectors in search of fresh voucher specimens, and breeders in search of gravid females, would likely have completed their activities.

Whether an individual undergoes a '*cockaynei*' or '*drumensis*'-type life cycle, may also depend on the emergence (part *i* or *ii*) from which it derived and hence the time

available to complete larval development, and on underlying genetic differences in growth rate (Robertson, 1980b). Similar considerations would apply to the offspring of second generation individuals developing under cool summers.

EVOLUTIONARY CONSIDERATIONS

P. aegeria probably reached Britain from Europe when the ice retreated after the Loch Lomond readvance of *c.* 10 000 B.P. (Dennis, 1977), though the history of subspecies *oblita* is not firmly established since the species can undergo dramatic changes in distribution over much briefer time scales, as within the present century (Barbour, 1986). However, while winter frost is rare in N.W. Scotland (Thomson, 1980), populations colonizing the region from the south would experience cooler and shorter summers and correspondingly longer daylengths, possibly resulting in a proportion of the progeny undergoing '*cockaynei*' and '*drumensis*' life cycles. Individuals undergoing the normal strategy would be likely to emerge too late in the season to breed, but those undergoing the '*drumensis*' strategy could yield progeny the following spring that in turn develop under a cool summer. Under such recurrent seasons, a strategy initially conditioned by parental effect might come to be intrinsically determined, and under the prevailing seasonal daylengths, show a concomitant shift in the critical photoperiod for pupal diapause to longer daylengths; although the precise mechanism by which such shifts in the 'norm of reaction' come about is a matter for investigation. In Scotland, *P. a. tircis* appears to be extending its range down the Great Glen from deciduous forest in the north-east to cooler pine forests more south-west. An examination of responses along the cline to particular climatic regimes could help us understand whether there is a rapid adaptation in the species to minor climatic shifts (Barbour, 1986).

One of Waddington's (1961) experiments selected for '*bithorax*' flies (where the metathorax develops wings in place of halteres) produced by exposing the eggs to ether, but Ho *et al* (1983) obtained similar increases in the incidence of *bithorax* using highly inbred lines of negligible genetic variability and without applying selection; moreover, despite reduced fecundity and survival in *bithorax*. These findings appear to involve progressive changes in maternally imposed organization of the egg surface cytoplasm, which may further condition changes in nuclear gene expression (Ho *et al*, 1983). Since a study on pupal chilling in *P. aegeria* had shown more extreme development of '*cockaynei*' features among the F_1 at 14°C than in the cold-treated parents (Winokur & White, in prep.), comparable cytoplasmic effects could be involved in mediating lepidopteran evolution; although induced changes in sperm chromosomal DNA could represent a possible mechanism (cf. Vuillaume & Berkaloff, 1974).

Vuillaume & Berkaloff, working with the large white butterfly, *Pieris brassicae* L., had found that larvae administered LSD failed to undergo the usual pupal diapause under daylengths of 9 h or less, but that their progeny were resistant to corresponding doses of the drug. They suggested that LSD activates a detoxifying mechanism in the parent butterfly that is passed on to its offspring. Moreover, since the resistance of the progeny to LSD proved greater when just the male parent had been treated than when the female alone had been treated, Vuillaume & Berkaloff suggested that inheritance of the detoxification mechanism is mediated via induced changes in sperm chromosome structure.

Alternatively, adaptation might involve the process of gene amplification, in which multiple copies of appropriate DNA sequences are generated and incorporated within the genome (see Pollard, 1988). Gene amplification, for instance, is known to

be involved in the rapid acquisition by insect populations of insecticide resistance, and appears to be part of the physiological repertoire of all cells (Ho, 1988). Moreover, the environmental stimulus may actually stabilize those cells in which the appropriate genes are being amplified, in which respect the environment, rather than selecting for a pre-existing genetic variant, is selecting for a cytogenetic response (Ho, 1988). For example, it was above suggested that in *P. a. oblita*, adult size was compromised to a lesser degree by rearing at 14° versus 17°C than in *P. a. tircis*, because the former had become metabolically adjusted to enable more efficient growth at lower temperatures. Should this have involved the amplification of genes appropriate for efficient nutrient assimilation and metabolism, and also present in *P. a. tircis* but in a lesser complement (as opposed to selection for a gene just improving metabolism at 14°C), then this would explain *P. a. oblita* continuing to attain the greater size at 17° and 20°C. However, when egg yields and fertility were compared, performance was severely compromised at 14°C compared to 17°C in *P. a. oblita* (Sibly *et al*, in prep.), the reverse of what might be expected should *P. a. oblita* be carrying the greater metabolic gene complement. An alternative explanation therefore, is that in S. England, where the hotter summers and more intense solar radiation force high metabolic rates with a concomitant risk of tissue damage, *P. a. tircis* has responded by amplifying genes appropriate for coping with rapid metabolic turnover. Not only would this protect such individuals from heat stress, but the amplified complement of metabolic genes may enhance the allocation of metabolic resources to other functions such as reproduction. Should this have involved genes also present in *P. a. oblita* only in lesser complement (as opposed to a gene enhancing performance specifically at 20°C), then this would explain *P. a. tircis* continuing to grow faster (and accordingly to produce smaller adults) yet remaining more fecund than *P. a. oblita* at also 17° and 14°C. The initial adjustment to warmer conditions however, would likely have required a shift in the allocation of metabolic resources from growth (and reproduction) to cytogenetic restructuring, leading to an initial loss of condition, as occurs with flax plants transplanted between culture media (Cullis, 1983). Indeed, it is noteworthy that among *P. a. oblita* undergoing larval aestivation at 20°C (warmer than normally experienced in the field, Table 1), a number of individuals showed varying degrees of wing pattern abnormality (Plate I Fig. 21), indicative of developmental stress. Furthermore, a shift in resource allocation to cytogenetic restructuring could explain why rearing at 20°C did not bring fecundity up to the level exhibited by *P. a. tircis*. However, cytogenetic and molecular studies will be required before firm conclusions are drawn. Such considerations, as well as those pertaining to the spatial and temporal heterogeneity of ancestral environments (Sibly & Atkinson, 1994), are particularly critical if the success of introduction attempts necessitating stock of disparate origin, the capacity of species to expand their ranges, and the impact of rapid climatic shifts as with global warming, are to be accurately predicted.

Reciprocal crosses between stocks (e.g. *oblita* female × *tircis* male, *tircis* female × *oblita* male) with pure crosses as controls, and between cohorts reared under different culture regimes (e.g. 14°C female × 20°C male, 20°C female × 14°C male) could identify more specifically the roles of maternal (cytoplasmic) effect, genotype, and environment, in determining life history strategy and consequently adult size and pattern. A high incidence of pattern abnormalities in such crosses might disclose nuclear/cytoplasmic incompatibilities, important in predicting the effects of mixing between locally adapted populations, as could occur between *P. a. tircis* and *P. a. oblita* south-west of the Great Glen.

ACKNOWLEDGEMENTS

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SHORT COMMUNICATION

***Swammerdammia compunctella* H.-S. (Lepidoptera: Yponomeutidae), in Merthyr Tydfil, Glamorgan, S. Wales.**—Whilst curating G. Fleming's collection of Lepidoptera (accession number NMW.1927.644) in the National Museum of Wales, Cardiff, I came across a series of *Swammerdammia* that he had named as *S. caesiella* (Hübn.). The series was collected from the area of Merthyr Tydfil between 1920 and 1926, in the months of June and July. Of the twenty specimens, 18 were re-determined by myself as *S. albicapitella* (Scharf), and the remaining two as *S. compunctella* (H.-S.). My determinations were confirmed by David Agassiz at the 1994 BENHS exhibition.

It would appear that *S. compunctella* has not previously been recorded in Glamorgan (VC41), and possibly not even from Wales (Agassiz, 1987). It would therefore be useful to search for the larvae in the spring on young Rowan trees.

It is also worth noting that the G. Fleming collection contains a great number of micro-Lepidoptera, mostly from South Wales, the records of which have probably never been published.

The full data from the two specimens are: Merthyr Tydfil, 22.vi.1925, and Merthyr Tydfil 25.vi.1926.—D. J. SLADE. c/o National Museum of Wales, Cathays Park, Cardiff CF1 3NP.

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